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TROPICAL SOCIAL PARASITES IN THE ANT GENUS *PHEIDOLE*, WITH AN ANALYSIS OF THE ANATOMICAL PARASITIC SYNDROME (HYMENOPTERA : FORMICIDAE)

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SUMMARY

Because social parasites are relatively rare in tropical ant faunas, new or poorly known forms deserve special attention. Two *Pheidole* species evidently parasitic on *P. indica* are here described as new species from India *(P. lanuginosa, P. parasitica)*, while a previously known northern South American form, *P. microgyna* Wheeler, is redescribed and evaluated as a possible parasite of *P. minutula* or a closely related host species.

Next, all of the nine certain or likely social parasites of *Pheidole* known worldwide are compared, and an anatomical parasitic syndrome is identified through character state analysis. The nine species appear to be independently evolved. The parasitic character states have tended to evolve within each of these species at different rates, and hence the evolution is interpreted as having been not only parallel among species but mosaic in nature within species (see *table I*). In spite of the lesser irregularities in this pattern, an overall trend is evident : the first changes to occur were loss of the worker caste (a loss still incomplete in the overall slightly modified *P. inquilina*), reduction of size, lengthening of the scape, reduction of sculpturing on the body surface, and broadening of the postpetiole. These shifts were followed by reduction of the mandibles and the segments of the funiculus.

The genera *Anergatides* and *Bruchomyrma*, each based on a single extremely advanced species, are placed in synonymy under *Pheidole*. The problematic genera *Hagioxenus*, *Parapheidole*, and *Sifolinia* are compared with *Pheidole* and their status evaluated.

The greater known diversity of parasitic ants in the temperate zones, as compared with the tropics, remains a key problem in the study of ant evolution. Whether the difference is genuine or an artifact of differential sampling cannot be determined until more intensive collecting is undertaken in the tropics.

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ZUSAMMENFASSUNG

Tropische Sozialparasiten der Ameisengattung Pheidole, **mit einer Analyse des anatomischen Parasiten-Syndroms**

Da Sozialparasiten verhältnismässig selten in tropischen Ameisenfaunen vorkommen, verdienen neue oder wenig bekannte Formen besondere Beachtung. Zwei neue *Pheidole* Arten aus Indien *(P. lanuginosa, P. parasitica)*, die offenbar parasitisch bei *P. indica* leben, werden hier erstmals beschrieben. Eine andere, bereits bekannte Art aus dem nördlichen Südamerika (*P. microgyna* Wheeler), wird neu beschrieben. Diese Art lebt möglicherweise als Parasit bei *P. minutula* oder bei einer nahe verwandten Wirtsart.

Alle der neun nachgewiesenen oder vermuteten sozialparasitischen Arten von *Pheidole*, die bisher weltweit bekannt wurden, werden vergleichend morphologisch untersucht, und auf Grund einer taxonomischen Merkmals-Rang-Analyse (character state analysis) wird ein anatomisches Parasiten-Syndrom vorgestellt. Die neun Arten scheinen sich unabhängig von einander entwickelt zu haben. Die parasitischen Merkmalszustände scheinen unabhängig und mit einer unterschiedlichen Evolutionsrate innerhalb jeder Art entstanden zu sein. Daher darf man annehmen, dass sich die Merkmale unter den Arten sowohl durch Parallel- als auch Mosaik-Evolution entwickelt haben. Der Gesamt-Trend ist jedoch offenkundig: die ersten Veränderungen waren der Verlust der Arbeiterkaste (noch unvollkommen bei der insgesamt nur wenig abgewandelten *P. inquilina*), Verringerung der Grösse, Verlängerung des Scapus, Verringerung der Körperoberflächenskulptur, und Verbreiterung des Postpetiolus. Diesen Veränderungen folgte die Verkürzung der Mandibeln und der Segmente des Funiculus.

Die Gattungen *Anergatides* und *Bruchomyrma*, die beide jeweils auf einer einzigen Art beruhen, werden als synonym *Pheidole* zugeordnet. Die Gattungen *Hagioxenus, Parapheidole* und *Sifolinia* werden mit *Pheidole* verglichen und ihr Status bewertet.

Die grössere Vielfalt der parasitischen Ameisen in den gemässigten Zonen im Vergleich zu den Tropen, bleibt ein Schlüsselproblem in der Erforschung der Ameisenevolution. Ob der Unterschied der Wirklichkeit entspricht, oder ob er das Resultat unterschiedlicher Sammelintensität ist, kann erst entschieden werden, wenn auch in den Tropen intensiver gesammelt wird.

INTRODUCTION

For 180 years a sequence of gifted entomologists, from P. HUBER, A. FOREL, F. SANTSCHI, W.M. WHEELER, and C. BRUCH in past generations to N. KUSNEZOV, H. KUTTER, A. BUSCHINGER, and others in more recent time, have steadily and literally unearthed an astonishing wealth of social parasites among the ants. The species discovered display among themselves virtually every conceivable form of exploitation of the host colonies, including xenobiosis, trail parasitism, slavery, temporary social parasitism, and inquilinism up to and including loss of the worker caste and extreme anatomical degeneration of the reproductive forms (reviews and recent literature in BRUCH, 1931 ; KUSNEZOV, 1951 a, b ; KUTTER, 1969 ; WILSON, 1971 ; BUSCHINGER, 1974 ; BUSCHINGER *et al.*, 1980 ; BUSCHINGER and WINTER, 1983).

From this research something of a paradox has emerged. The greatest

frequency of social parasites, both in new species discovered per year and overall percentage of ant species known to be parasitic, occurs in the north temperate zone and especially in the colder portions, where the smallest total ant fauna exists. However, this is also the region where the most diligent entomologists have concentrated their efforts. Thus an important question is raised: is the relative scarcity of social parasites known from the tropics a reflection their true proportionate rarity, or is it an artifact of the difference in collecting intensity? In other words, is the paradox real? Any new information on tropical parasitic species is therefore of more than average interest.

In the course of recent preliminary work toward a revision of the New World species of *Pheidole*, I surveyed several thousand series in the Museum of Comparative Zoology, Harvard University, and Museu de Zoologia, Universidade de São Paulo, originating from around the world and representing about five hundred species. Three of the tropical forms show evidence of being parasitic. I describe them below to put their existence on the record and to call attention to the excellent possibility for additional such discoveries in this large, exceptionally diverse genus.

DESCRIPTIONS OF NEW AND LITTLE KNOWN SPECIES

Pheidole lanuginosa **Wilson, new species**

Diagnosis (queen). Body of "normal" *Pheidole* form but exceptionally small (*e.g.*, head width 0.75 mm) and with short, rounded head. Also, the body surface uniformly smooth and dully shining, except for several longitudinal costulae between the eye and antennal fossa. Antennal scapes long, about equal in length to head width and in repose exceeding the occipital corners by approximately one-third their length. Pilosity moderately abundant over the entire body and mostly appressed or nearly so, with many of the hairs strongly curved and even hooked at the end, giving the ant a distinctive "woolly" appearance, hence the scientific name proposed for it here. An apparent social parasite of *Pheidole indica* Mayr.

Holotype queen. Museum of Comparative Zoology. An alate specimen, closely resembling the paratype queen illustrated in *figure 1.* Head width exclusive of eyes 0.75 mm, head length (anterior clypeal margin to occipital border) 0.78 mm, scape length 0.76 mm, eye length 0.31 mm. Mandibles well-formed, with a large apical and a large preapical tooth followed by 6 evenly spaced smaller teeth occupying the remainder of the masticatory border. Anterior clypeal border very feebly convex; entire clypeal dorsal surface also feebly convex. Hypostomal border evenly concave, lacking teeth. Antenna 12-segmented; the well-developed 3-segmented club occupies almost exactly half the length of the funiculus. With the exception of 2-3 parallel carinulae that run longitudinally between the inner border of the compound eye and the antennal fossa, the body is smooth to lightly shagreened and dully shining to subopaque over most of its surface. The pilosity is moderately abundant; the majority of hairs are relatively thick (compared with those of other *Pheidole* species) curving downward, and appressed to decumbent (parallel with the surface to rising 45° from the surface). Some hairs, such as those on the fore coxae, propodeal spines, and postpetiolar venter, are bent at right angles or hooked at the end. Color uniformly pale yellowish brown. This specimen is fully alate.

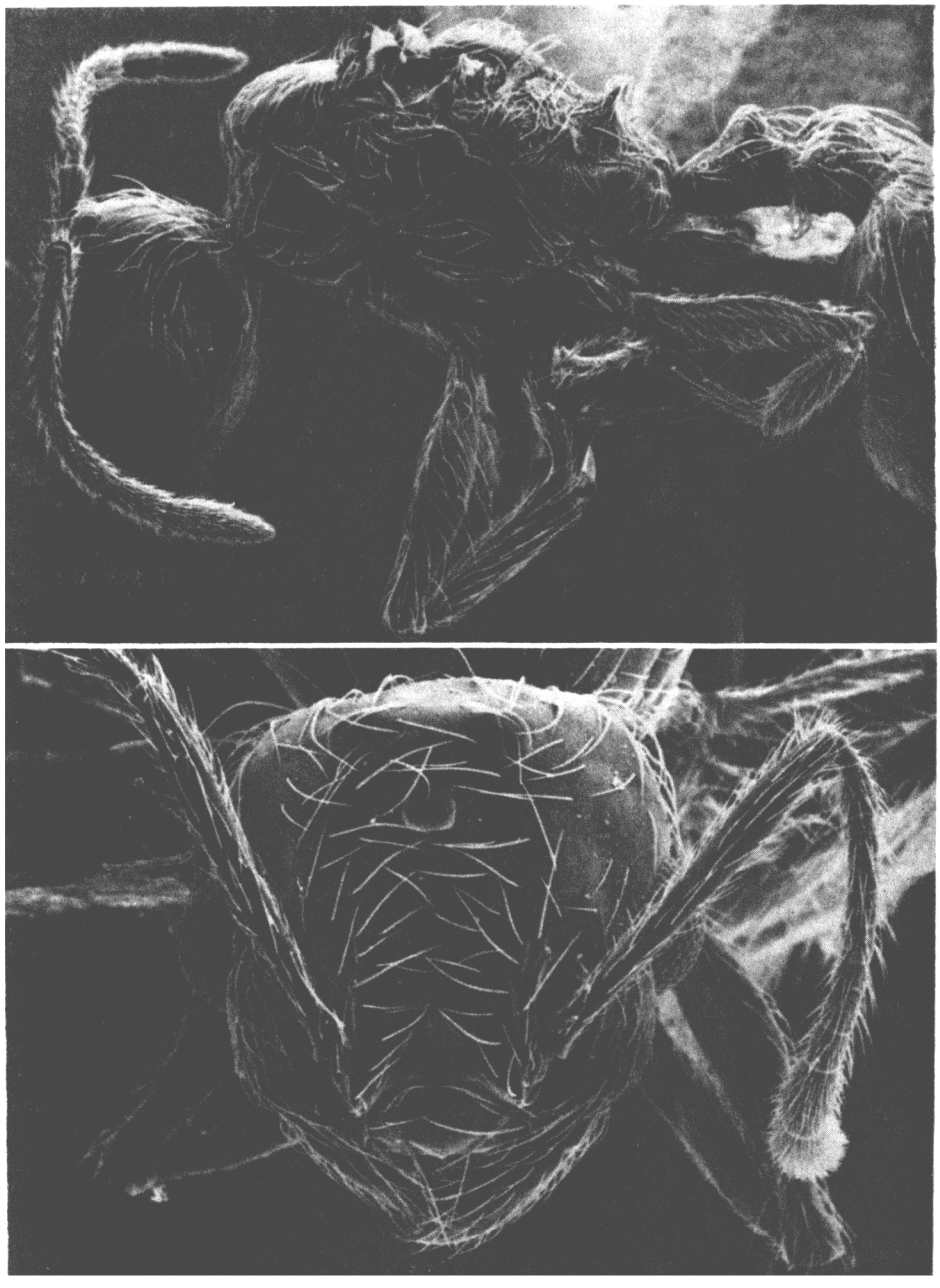

Fig. 1. — Paratype queen of the Indian parasitic ant species *Pheidole lanuginosa* n. sp., side view of body *(upper)* and frontal view of head *(lower)*.

Abb. 1. — Paratypus der Königin der parasitischen Ameisenart aus Indien, *Pheidole lanuginosa* n. sp.; Seitenansicht *(oben)*, Vorderansicht des Kopfes *(unten)*.

Paratype queen (fig. 1). Head width 0.77 mm, head length 0.76 mm, scape length 0.70 mm, eye length 0.31 mm. Overall closely similar to the holotype. Apparently newly dealated, possibly during capture: long wing stubs, including some hyaline portions, are still present.

Male paratypes, 2 specimens *(fig. 2).* Head width (including eyes) 0.66, 0.68 mm; head length 0.56, 0.60 mm; scape length 0.20, 0.18 mm; eye length 0.24, 0.27 mm. Mandibles with a well developed masticatory border bearing an apical, subapical, and three evenly spaced and smaller posterior teeth. Pilosity similar to that of queen, except that a majority of hairs stand 45° or more away from the surface and almost none are completely appressed. Many on the propodeum and petiole are hooked or sinuous. Color yellowish brown, similar to that of the queen.

Jorhat, Assam, India: 2 queens and 2 males (A.C. COLE, March 1944). Collected with minor and major workers of *Pheidole indica* Mayr, a widespread Asiatic species.

In addition to the association with *P. indica* just noted, the parasitic nature of *P. lanuginosa* is suggested by the following combination of anatomical features of the queens: small size, smooth body surface, elongate scapes, relatively thin, lightly colored exoskeleton, and appressed to decumbent curving pilosity. Most of these traits cannot be considered individually very

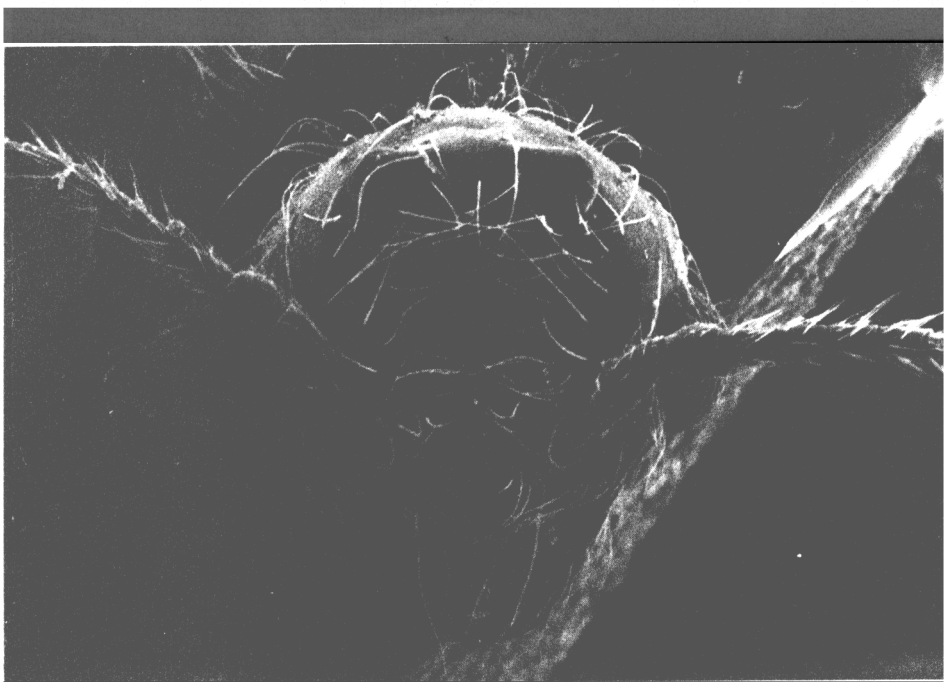

Fig. 2. — Paratype male of *Pheidole lanuginosa* n. sp., frontal view of head.

Abb. 2. — Paratypus des Männchens von *Pheidole lanuginosa* n. sp.; Vorderansicht des Kopfes.

significant, but as an ensemble they are strongly indicative. The pilosity, however, is of special interest by itself. It deviates from pilosity of other *Pheidole* species in the same way that thick, appressed, and sinuous hairs distinguish the parasitic species *Formica ciliata* and *Lasius crinitus* from their many nonparasitic congeners.

The phylogenetic origin of *P. lanuginosa* cannot be deduced from existing data. The queens are very different in many respects from those of the host species, *P. indica.* Three *indica* queens examined from southern China are much larger (head widths 1.4-1.6 mm). As in the case of most other nonparasitic *Pheidole* species, they also share many of the traits of the conspecific major worker caste: heavy, dark reddish exoskeleton; predominantly erect and suberect pilosity with no hairs curved or hooked; dense, rugoreticulate sculpturing over most of the head, alitrunk, petiole, and postpetiole; relatively short scapes, failing to attain the occipital border; and 5 well-developed hypostomal teeth. Emery's Rule, that social parasites tend to be derived from the host species or a closely related form. cannot be discounted in this case. The relatively large differences between *lanuginosa* and *indica* might still easily be the result of reduction during the transition to a parasitic way of life. Even the genal costulae of the *lanuginosa* queen can be regarded as consistent with the heavier genal rugae of the *indica* queen.

A potentially important character that I have recently identified in *Pheidole* males is the form of the mandible, which varies dramatically from species to species. The *lanuginosa* male has the trait tentatively interpreted to be the primitive state: a broad masticatory blade with an apical, subapical, and three smaller, more posterior teeth of similar size distributed evenly along the border. An *indica* male examined from Shikoku, Japan, has a similar but perhaps somewhat more advanced mandibular form, in which the subapical tooth is missing and the two central teeth are fused.

Pheidole parasitica **Wilson, new species**

Diagnosis (queen). A small species displaying the following advanced features apparently associated with inquilinism: head capsule nearly perfectly circular in frontal view, reduced in size relative to remainder of body; mandibles greatly reduced in size and structure, so that the masticatory border is 0.1 mm long and retains only the apical tooth; antennal scapes elongate, much longer than the head width and in repose exceeding the occipital corner by more than twice their length; antenna 12-segmented but lacking a distinct club; propodeum unarmed and dorsoventrally flattened, its entire basal and declivitous surfaces forming a single oblique plane; petiolar node reduced, merging almost imperceptibly into the peduncle; postpetiole trapezoidal from above, its broad posterior face applied fully over the first gastric segment; and the entire body surface, with the exception of several carinulae between the eye and antennal fossae and on the lateral propodeal surface, smooth and moderately shining.

P. parasitica somewhat resembles *P. acutidens* of Argentina and *P. kohli* of Zaire, clearly through evolutionary convergence, but it is less extreme in several key traits: its mandibles are less reduced, so that their tips still cross in repose; the number of

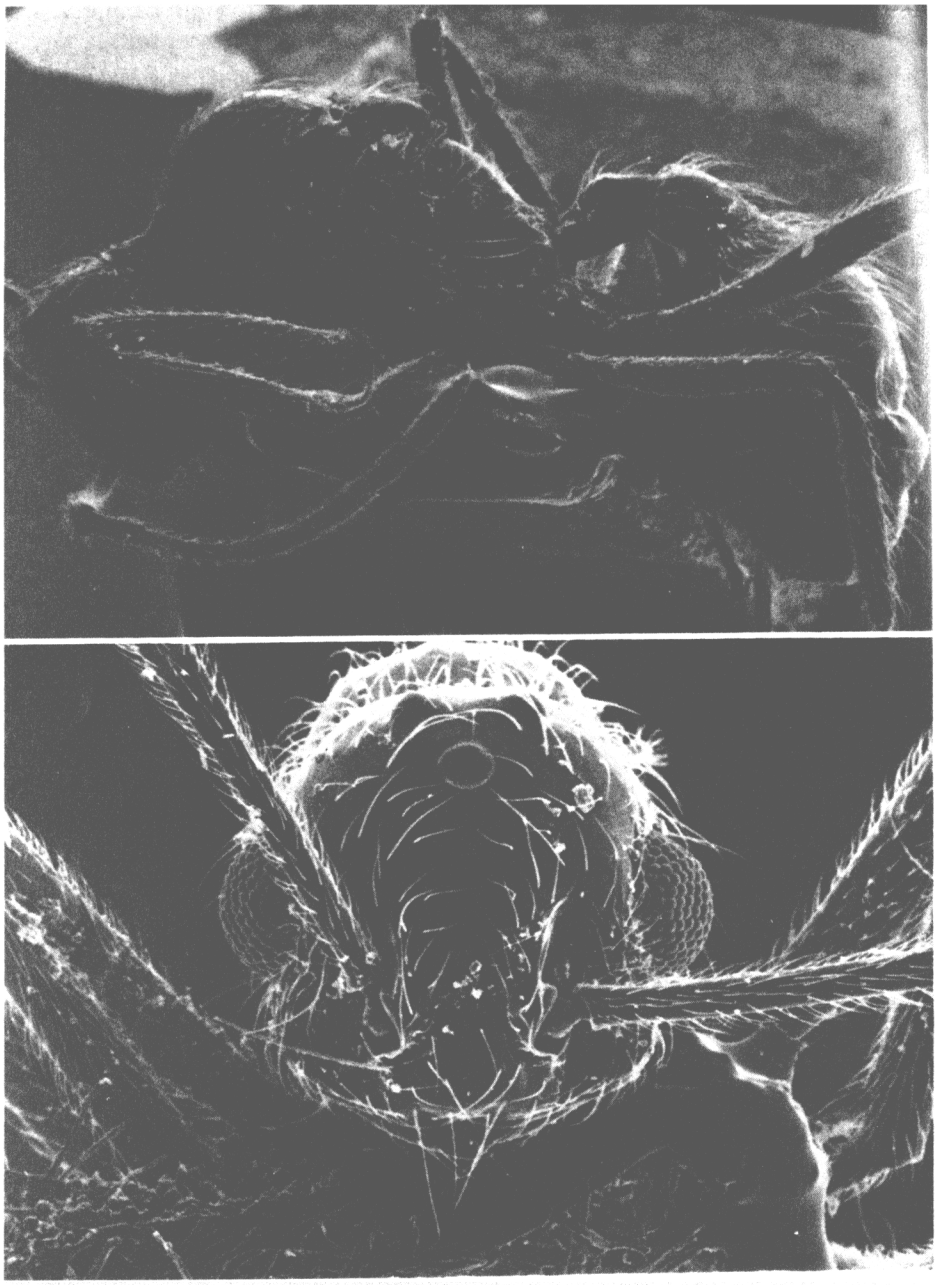

Fig. 3. — Paratype queen of the Indian parasitic ant *Pheidole parasitica* n. sp., side view of body *(upper)* and frontal view of head *(lower)*.

Abb. 3. — Paratypus der Königin der parasitischen Ameise *Pheidole parasitica* n. sp. aus Indien ; Seitenansicht *(oben)* und Vorderansicht des Kopfes *(unten)*.

antennal segments is not reduced (distinguishing *parasitica* from *acutidens*); the scutellum is not elevated nearly as much; the postpetiole is narrower; and the abdomen is much smaller relative to the remainder of the body.

Holotype queen. Museum of Comparative Zoology. An alate specimen, closely resembling the paratype illustrated in *figure 3.* Head width exclusive of eyes 0.60 mm, head length (anterior clypeal border to occipital border) 0.65 mm, scape length 0.84 mm, eye length 0.22 mm, length of masticatory border of mandible 0.10 mm. Anterior clypeal border feebly concave; dorsal surface of clypeus weakly convex. Hypostomal border evenly concave, lacking teeth. Antenna 12-segmented, but lacking a distinct club; the lengths of the segments from the funicular tip to and including the scape are 0.30, 0.14, 0.15, 0.15, 0.13, 0.10, 0.08, 0.06, 0.06, 0.07, 0.18, 0.84 mm respectively. The widths of the segments diminish gradually from the outermost funicular segment inward. Width of posterior postpetiolar border 0.40 mm, in striking contrast to the width of the posterior petiolar border, which is 0.18 mm. Four longitudinal carinulae are located between the eye and antennal fossa and two are on the lateral propodeal face; otherwise the entire body is smooth and moderately shining. A dense yellowish pilosity covers all of the body and appendages; the hairs are mostly decumbent to suberect (forming an angle near their base of 20-60° from the surface) and curving slightly downward; a few are either hooked, as on the occiput, or else sinuous, as on the petiolar node. Body uniformly medium brown, appendages light brown.

Paratype queens (fig. 3). Head widths range 0.57-0.62 mm. Overall closely similar in appearance to the holotype.

Chabua, Assam, India: holotype and 22 paratype queens, both alate and dealate (A.C. COLE, 24 July 1944). Calicut, Kerala, India: 1 alate and 1 dealate queen (A.B. SOANS, June 1969, "soil"). Both series were collected with minor and major workers of *Pheidole indica.*

The relationships of *P. parasitica,* like those of most other extreme parasitic ants, cannot be judged at this time with any degree of certainty. Even the generic placement is somewhat arbitrary, in view of the absence in the queen of the characteristic 3-segmented club. One possible clue is the persistence of carinulae on the genae (also found in *P. lanuginosa)* and lateral faces of the propodeum, which might be homologous to the rugae in the same locations in the host species *P. indica.*

Pheidole microgyna **Wheeler**

Diagnosis (queen). Resembling *P. minutula* Mayr but much smaller, close in size to the major worker caste, with head width only about 0.5 mm. Head short and rounded. Scape relatively long, in repose exceeding the occipital margin by a distance slightly greater than its own maximum width. Propodeum greatly flattened dorsoventrally, with basal and declivitous faces viewed in profile forming a single line broken by short blunt teeth that form 135° angles at their apex. Body surface almost entirely smooth and moderately to strongly shining.

Lectotype queen (newly designated). Museum of Comparative Zoology. A dealate specimen, closely resembling the paratype illustrated in *figure 4.* Head width exclusive of eyes 0.47 mm, head length (anterior clypeal border to occipital border) 0.65 mm, scape length 0.39 mm. Anterior clypeal border almost perfectly straight through most of its medial portion; dorsal surface of clypeus very weakly convex, almost flat. Hypostomal border deeply concave, lacking teeth. Antenna 12-segmented; antennal club

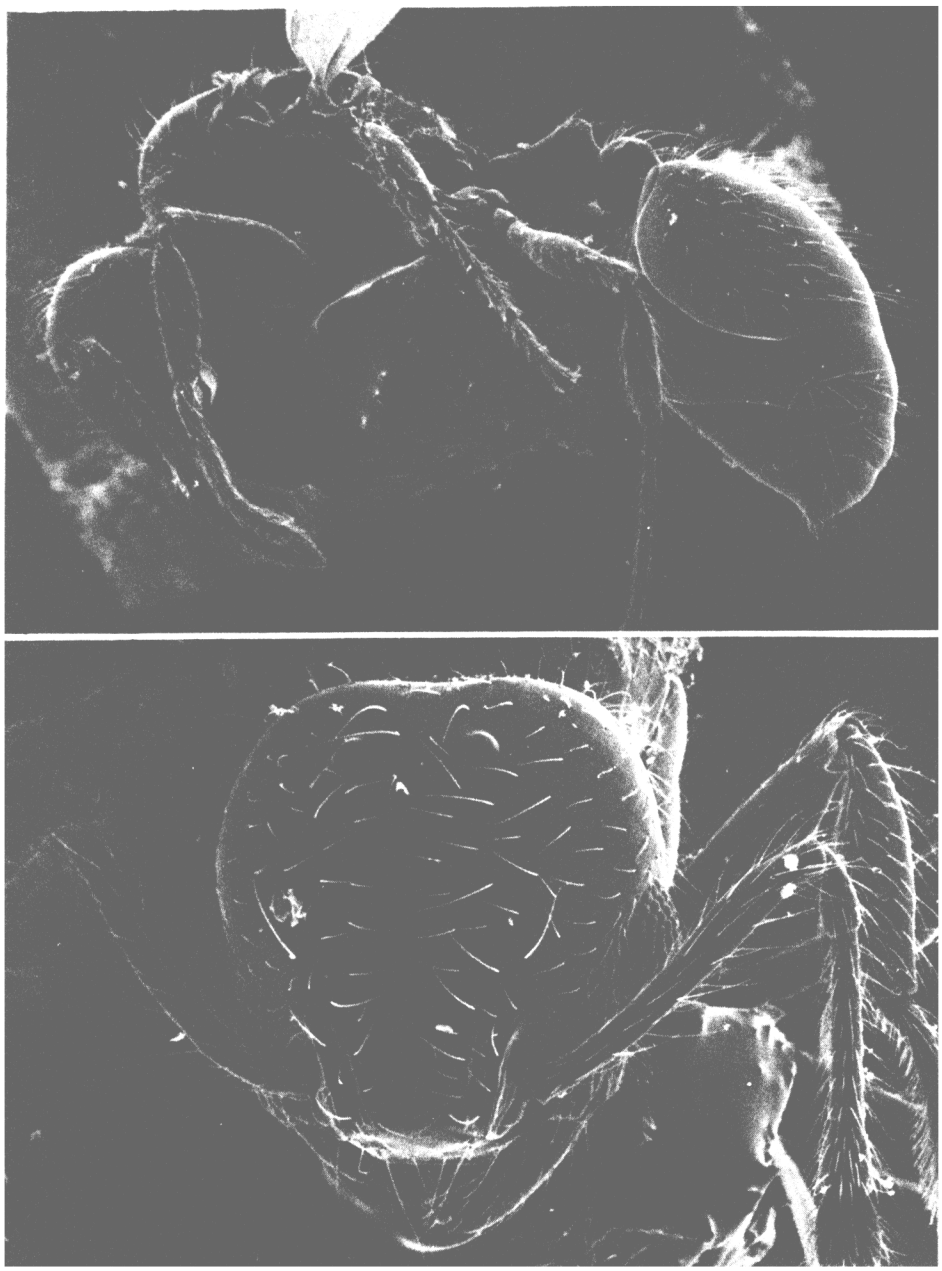

Fig. 4. — Paratype queen of the South American ant *Pheidole microgyna* Wheeler, a possible social parasite, side view of body *(upper)* and frontal view of head *(lower)*.

Abb. 4. — Paratypus der Königin der südamerikanischen Ameise *Pheidole microgyna* Wheeler, ein möglicher Parasit ; Seitenansicht *(oben)* und Vorderansicht des Kopfes *(unten)*.

distinct and 3-segmented, about as long as the remainder of the funiculus. Body smooth and shining, with the following exceptions: six longitudinal carinulae between inner margin of eye and antennal fossa; other carinulae scattered between the frontal carinae and frontal triangle and along the dorsal plane of the scutum; a patch of weak rugo-reticulum on the anterior half of the lateral pronotal face; and shagreening over the propodeum and petiolar peduncle. Pilosity moderately dense over entire body and appendages, consisting primarily of straw-yellow, thin, suberect to erect and slightly curving hairs. Body uniformly light reddish brown, appendages a moderately contrasting yellowish brown.

Paratype queens. Head width 0.46-0.48 mm. All are closely similar to the lectotype (see *fig. 4*).

Kartabo, Guyana: alate lectotype and 6 alate paratype queens (W.M. WHEELER, 25 August 1920, acc. no. 638; associated with minor workers of a species of the *P. minutula* group). Also paratype queen (W.M. WEELER, 31 August 1920, acc. no. 721; associated with 2 major workers of apparently the same species as the minor workers collected with the lectotype).

The name *Pheidole microgyna* is of marginal validity, having been scarcely mentioned by Wheeler in 1928 and then totally neglected in the literature for the next 50 years. Here is Wheeler's entire account: " In one minute and perhaps parasitic species (Ph. microgyna sp. nov), which I found in British Guiana, all three of the castes [queen, minor worker, major worker — E.O.W.] are nearly of the same size... if Ph. microgyna be really parasitic, the small stature of its queen is probably due to a secondary reduction, but if it is non-parasitic, we may be dealing with a very primitive condition ".

In rediscovering Wheeler's material in the Museum of Comparative Zoology at Harvard University, I have taken the step of describing it adequately under the same name used by Wheeler. It seems prudent to treat Wheeler's brief mention of the species in 1928 as the valid description, even through a case might be made for using a new name and ascription (but with potentially even greater confusion in the future). I trust that the species will be left as *P. microgyna* Wheeler for purposes of nomenclatural stability.

Associated workers. Of greater importance is the worker series collected with the *microgyna* queens and what they reveal concerning the biology of the queens. The minor and major workers are very similar to series of *P. minutula* Mayr from Tingo Maria, Peru (compared with a syntype by W.L. Brown), and series collected by Joseph Bequaert and myself at Belem and Manaus, Brazil, from the swollen leaf bases of the melastome understory shrub *Maieta guianensis.* The Belem series had been identified by Wheeler as *P. minutula* subsp. *folicola* Forel, but the differences do not seem very important. The *microgyna*-associated workers, on the other hand, have several significant morphological traits that would seem to distinguish them at the species level from *minutula.* As shown in *figure 5,* their propodeal spines are acute and upwardly curving (they are not only shorter and less acute but also quite straight in *minutula);* and the head of the major has shorter rugae on its anterior surface and is more shining.

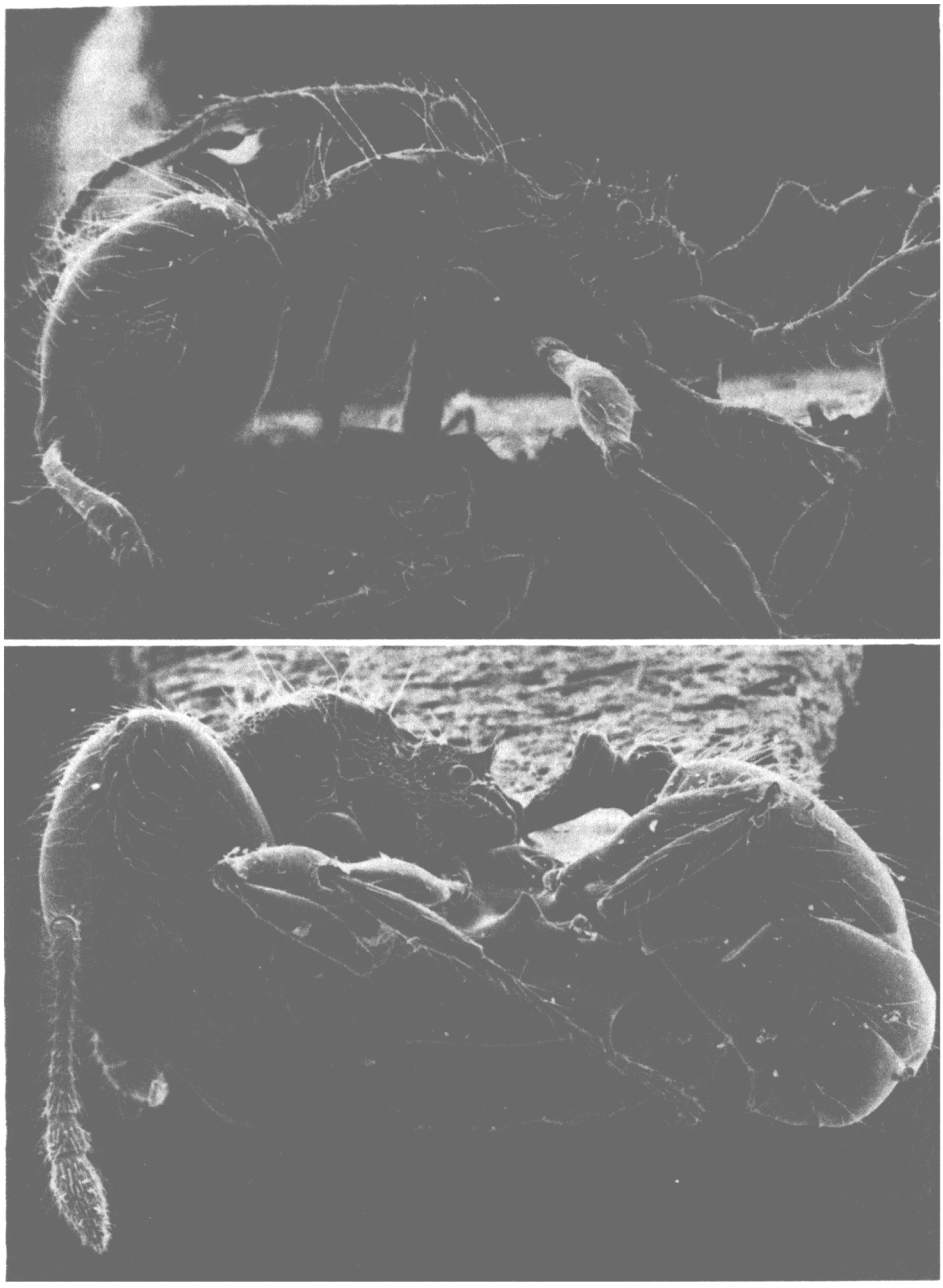

Fig. 5. — Workers of a species in the *Pheidole minutula* group found associated with *P. microgyna*. Upper, minor worker ; lower, major worker. Not in scale.

Abb. 5. — Arbeiter einer Art in der *Pheidole minutula* Gruppe, die zusammen mit *P. microgyna* gefunden wurden. Oben, " minor " Arbeiter ; unten, "major " Arbeiter. Nicht masstabsgetreu.

Overall, the minor and major workers associated with the *microgyna* queens are different enough to be tentatively regarded as representing a species distinct from *minutula*. It might seem to follow that they are the offspring of *microgyna* queens. However, a complicating factor is the existence in the Museum of Comparative Zoology of a series from Kalacoon, Guyana, of which the minor and major workers resemble those associated with *microgyna* at Kartabo and the queens are large forms closely similar to the Brazilian *minutula*.

The latter circumstance is consistent with the hypothesis that *microgyna* is a temporary social parasite of *minutula* or some related free-living species. The peculiar morphology of the *microgyna* queens also suggests such a life cycle. However, the mystery of the status of this remarkable form will not be solved until additional collections are made, permitting the taxonomy of the *minutula* group to be more fully clarified.

AN ANNOTATED LIST OF ADDITIONAL KNOWN AND POSSIBLE SOCIAL PARASITES OF *PHEIDOLE*

Pheidole acutidens (Santschi), *An. Soc. Cient. Argent., 94,* 248-251, *figures A-D* (1922). *Bruchomyrma acutidens.* Type locality: Alta Gracia, Córdoba, Argentina. Queen. Host: *Pheidole nitidula. Pheidole (= Bruchomyrma),* New synonymy.

BRUCH (1931) provided extensive notes on the ecology, behavior, life cycle, and anatomy of this remarkable workerless inquiline. The male is brachypterous and pupiform. The queen possesses many degenerate traits of her own. For example, the number of antennal segments in 11 queens I have examined varies from 9 to 11; in some cases the number differs on the antennae of the same individual. The instability of the trait is further evidenced by the fact that various degrees of fusion, from partial to complete, can be observed from one adjacent pair of segments to the next. The mandibles of the queen are reduced to tiny appendages, toothless, tapered to a blunt point at the end, and only 0.06-0.07 mm long. They leave a gap of 0.13 mm between their tips when in repose.

BROWN (1973) suggested the possibility of generic synonymy of *Bruchomyrma* under *Pheidole.* For reasons to be given in the later section on phylogeny, I am making this change as a formal step.

Pheidole argentina (Bruch), *Rev. Mus. La Plata, Buenos Aires, 33,* 271-275, *figures 1-8* (1932). *Gallardomyrma argentina.* Type locality: Alta Gracia (La Granja), Sierra de Córdoba, Argentina. Queen. Host: *Pheidole nitidula.* Generic synonymy by Brown W.L., in Meggers B.J. *et al.*, eds., *Tropical Forest Ecosystems in Africa and South America* (Smithsonian Institution Press), p. 180 (1973).

The queen of this workerless inquiline has an antennal conformation unique among ants: 10 segments with a well-developed, 1-jointed club. Bruch's account implies that this character state is uniform throughout the type series.

Pheidole elecebra (Wheeler), *Bull. Am. Mus. Nat. Hist. New York, 20,* 8-10 (1904). *Sympheidole elecebra.* Type locality: Manitou, Colorado. Queen, male. Host: *Pheidole ceres.* Generic synonymy by Brown W.L., in Meggers B.J. *et al.*, eds., *Tropical Forest Ecosystems in Africa and South America* (Smithsonian Institution Press), p. 185 (1973).

Pheidole inquilina (Wheeler), *Bull. Am. Mus. Nat. Hist. New York, 19,* 664-666, *figure 5* (1903). *Epipheidole inquilina.* Type locality: Colorado Springs, Colorado. Gynandromorph. Host.: *Pheidole pilifera* subsp. *coloradensis.* Generic synonymy by Cole A.C., *Ann. Ent. Soc. Amer., 58,* 173-175 (1965).

Pheidole inquilina is the least anatomically modified of the pheidoline social parasites (see *table I*). It is therefore not very surprising that both the minor and major workers have been discovered in addition to the usual queens and males (SMITH, 1940; COLE, 1965). However, these castes are evidently in a state of evolutionary decline. In 19 nests of the host species, *Pheidole pilifera coloradensis,* excavated by Cole, 8 contained a few individuals of *P. inquilina;* and of these, one nest yielded only a single minor worker of *inquilina,* and another nest one minor and one major worker. In all of the compound colonies *inquilina* was outnumbered by the host workers. Smith noted the close resemblance of the worker castes of the two species, and suggested that *inquilina* was derived in evolution from *pilifera* or a related species. In other words, Emery's rule is exemplified.

The persistence of both worker castes in this relatively primitive inquiline offers an excellent opportunity for the study of retrograde evolution. It would be especially useful to learn whether the *inquilina* workers possess a full repertory of social behavior, or whether they have surrendered some part of colony maintenance to the host worker force.

Pheidole lanuginosa Wilson, new species. India. See previous description.

Pheidole microgyna Wheeler, *J. Exp. Zool.* (Philadelphia), *50,* 186 (1928). Type locality: Kartabo, Guyana (British Guiana). Queen. Host.: possibly *Pheidole minutula* or related species. See previous discussion in the present article.

Pheidole neokohli Wilson, Nom. Nov., N. Comb. for *Anergatides kohli* Wasmann, *Ent. Mitt. Berlin, 4,* 279-288, pl. 7-8 (1915). Type locality: Saint Gabriel, nr. Kisangani, Zaire (Stanleyville, Congo). Queen, male. Host · *Pheidole megacephala. Pheidole (= Anergatides),* New synonymy.

This species superficially resembles *P. acutidens* of Argentina and rivals it in the number of its extreme parasitic modifications. The queens and males, with their rounded heads, reduced (almost invisible) mandibles, and enlarged, globose abdomens (especially in the males), are vaguely reminiscent of small, yellowish brown spiders.

As in *acutidens*, the mandibles are greatly reduced. They are toothless, tapered to a blunt point at the tip, and only 0.14 mm long, so that when they are closed they leave a gap of 0.15 mm across the clypeal border and lower mouthparts. They also bear a unique structure: an elliptical pit on the outer surface near the base. The pit is 0.05 mm long and 0.02 mm wide, and it appears outwardly to be glandular in nature. The thorax is more extreme in form than that of *acutidens*. The frontal and dorsal faces of the pronotum meet in a right angle, and the scutellum is raised into a narrow, conspicuous hump 0.20 mm high but only 0.16 mm long when measured along the lateral line of the base.

The male is pupiform, with large everted genitalia. Its postpetiole is greatly expanded and attached along the entire broad posterior surface to the large first gastric segment. The male is also unusual in possessing only 12 segments in the antennae, as opposed to 13 as in all other known *Pheidole*.

The justification for the synonymy of *Anergatides*, a monobasic genus originally constructed for *kohli*, will be given in the phylogenetic section to follow. Transfer of *Anergatides kohli* to *Pheidole* makes it a secondary homonym of the African *Pheidole kohli* Mayr (1901), requiring the erection of the new name provided here (*P. neokohli* Wilson).

Pheidole parasitica Wilson, new species. India. See previous description.

Pheidole symbiotica (Kusnezov), *Mem. Mus. Entre Rios, Argentina, 29* (Zool.), 1-30, *figures 1-10* (1951). *Eriopheidole symbiotica.* Type locality: Parque General San Martin, Entre Rios, Argentina. Queen, male. Host: *Pheidole obscurior.* Generic synonymy by Brown W.L., in Meggers B.J. *et al.*, eds., *Tropical Forest Ecosystems in Africa and South America* (Smithsonian Institution Press), p. 180 (1973).

Kusnezov's field and laboratory research showed that *P. symbiotica* is a workerless inquiline of the host species. He correctly pointed out that the queen is much less modified anatomically than *P. acutidens, P. argentina* and some of the other workerless parasites in and around *Pheidole*.

PROBLEMATIC GENERA AROUND *PHEIDOLE*

Hagioxenus schmitzi Forel, *Ann. Soc. Ent. Belg., 54,* 8-9 (1910). Type locality: Jerusalem. Host: unknown.

The unusual species *Hagioxenus schmitzi*, described by FOREL (1910) from a single alate queen collected in Jerusalem, should be reexamined with reference to its possible parasitic status and relationship either to *Pheidole* or, as noted by W.L. BROWN (in Ettershank, 1966), to *Monomorium*. The specimen was collected in a nest of *Tapinoma erraticum*. Being alate, it is not a strong candidate for a parasite of that dolichoderine species. But it has at least some traits expected of a parasitic *Pheidole* : 12-segmented antenna with a 3-segmented club (characteristic of *Pheidole* generally), small body size, rounded head, unarmed propodeum which is also flattened and lacking distinct division into basal and declivitous faces, thickened petiole and postpetiole, and shining body surface. On the other hand the scapes do not reach the occipital border, and the body color is predominantly brown, a darker color not encountered in other pheidoline parasites. The petiole and postpetiole bear ventral processes, which are atypical of *Pheidole*. Of uncertain significance is the large, flat clypeus and indistinct frontal areas, perhaps overemphasized by Forel as a character state of generic rank.

Hagioxenus mayri (Forel), *Zool. Jahrb.* (suppl.), *15*, 1-57 (1912). Type locality : Poona, India. Host : *Pheidole latinoda*. *Rhoptromyrmex mayri* Forel ; generic transfer by Brown W.L., *Pilot Register of Zoology*, No. 19 (1964).

The Indian *H. mayri* is an even more promising candidate than *H. schmitzi* to be a pheidoline (and possibly a member of *Pheidole)*, because of its apparent parasitic association with *Pheidole latinoda* : « mit *Pheidole latinoda* zusammen von Herrn R. Wroughton gesammelt » (FOREL, 1912). As BROWN (1964) notes, the resemblance of the species to *Hagioxenus schmitzi* could be due to convergence, and its phylogenetic origin is wholly conjectural. The distinguishing traits of *H. mayri* include the following : scapes exceeding occipital border by one-third their length ; body wholly smooth and shining ; and body and appendages covered by thick, standing hairs.

Parapheidole oculata (Emery), *Boll. Soc. Ent. Ital., 3*, 276-277 (1899). *Aphaenogaster oculata*. Queen, a unique specimen. Type locality : Baie d'Antongil, Malagasy Republic (Madagascar). Host : unknown. *Parapheidole* Emery, *Rend. Accad. Sci. Bologna*, 1914-15, p. 68 (type species : *Aphaenogaster oculata* Emery).

Until the unique type can be restudied, and perhaps additional collections made in Madagascar, the validity and phylogenetic position of this problematic genus are insoluble. Its status as a social parasite, suggested by several authors in the past, is also under question. As noted in *table I*, *Parapheidole oculata* possesses few traits of the parasitic syndrome. Most suggestively, the queen is relatively large in size (total length 5.25 mm, scape length 1.4 mm)

in contrast to the confirmed pheidoline parasites. I have included it here for completeness and to call attention to the need for its rediscovery and further study.

Sifolinia laurae Emery, *Rend. Accad. Sci. Bologna,* 1906-07, p. 49. Type locality: Siena, Italy. Queen. Host: unknown.

It seems safe to remove *Sifolinia laurae* Emery, based on a single queen collected at Siena, Italy, from the roll of possible pheidoline parasites, the status suggested earlier by EMERY (1921) and BERNARD (1968). I agree with W.L. BROWN (1973) that it is a *Myrmica.* The holotype queen is close to other members of that genus in conformation of the funiculus, propodeum, and petiole and postpetiole. In particular, the latter segments possess ventral processes of the kind found in some *Myrmica* and *Leptothorax* but not, so far as I know, in any *Pheidole* or social parasite of *Pheidole.*

Table I. — Character states associated with social parasitism in known and possible parasitic species in *Pheidole,* as well as the problematic genus *Parapheidole.* X, present; —, absent.

Tabelle I. — Merkmalszustände, die mit Sozialparasitismus assoziiert sind, bei bekannten und vermuteten sozialparasitischen Arten der Gattung *Pheidole,* sowie bei der problematischen Gattung *Parapheidole.* X, vorhanden; —, nicht vorhanden.

Species	Small size	Loss of worker caste	Occiput rounded	Scapes elongated	Antennal club reduced	No. of antennal segments reduced	Mandibles reduced	Body surface shining	Propodeum reduced	Color lightened	Postpetiole broadened
Pheidole inquilina	X	—	—	X	—	—	—	—	—	—	X
P. lanuginosa	X	?	X	X	—	—	—	X	—	X	—
P. symbiotica	X	X	X	X	X	—	—	X	—	—	X
P. elecebra	X	X	X	X	—	—	—	X	—	X	X
P. microgyna	X	?	X	X	—	—	—	X	X	X	—
P. argentina	X	X	X	X	X	X	X	—	X	X	—
P. parasitica	X	X	X	X	X	—	X	X	X	X	X
P. kohli	X	X	X	X	X	—	X	X	X	X	X
P. acutidens	X	X	X	X	X	X	X	X	X	X	X
Parapheid. oculata	—	?	X	X	—	—	X	—	—	X	—

DISCUSSION

In *table I* are noted the presence or absence of 11 anatomical character states that appear to be associated with social parasitism in *Pheidole*, and in many other ant genera as well. All of the nine known or likely social parasites in *Pheidole* are specified, from a direct study I have made of specimens of every species except *argentina* (this form is described with exceptional thoroughness by BRUCH in his 1932 article). The identification and designation of primitive and derived character states is in accord with widely accepted procedures of phylogenetic systematics, including cladistic analysis (see, for example, WILEY, 1981).

The matrix is ordered from top to bottom, that is, from *inquilina* to *acutidens*, according to the increasing parasitic specialization of the species. In each case, the positive character state is provisionally considered derived from the more primitive alternative state or set of states found in the hundreds of other species of *Pheidole*. Such can be safely assumed to be true for loss of the worker caste, lengthening of the scape, reduction of the number of antennal segments, and reduction of the mandibles and propodeum. It is less certain in the cases of the reduction of queen size, rounding of the occiput, reduction of sculpturing (producing a shiny surface), and lightening of color. Two forms of postpetiolar broadening occur and are lumped together in *table I :* an extreme widening of the node into conules, which may or may not be derived, and a simultaneous widening of the segment and its complete attachment posteriorly to the first gastric segment, which is almost certainly derived.

An examination of the matrix reveals two apparent phylogenetic trends of interest :

1) The character states were often not acquired in concert ; in other words, there was a substantial amount of mosaic evolution.

2) The earliest changes to occur were loss of the worker caste, reduction of size, rounding of the occiput, lengthening of the scape, loss of body sculpture, and broadening of the postpetiole. These shifts were followed by reduction of the funicular segments, including the 3-segmented club, and of the mandibles.

We have only begun the exploration of social parasitism in the huge genus *Pheidole*, which is cosmopolitan in distribution, contains over 1 000 named forms, and probably exceeds *Camponotus* in abundance of colonies in most habitats (WILSON, 1976).

Where do most of the parasitic species of *Pheidole* occur ? I will be so bold as to predict that a large majority remain undiscovered, and that most of them occur in the tropics. More precisely, the largest absolute numbers are likely to occur in the tropics, although a higher *percentage* of the

temperate zone species may be social parasites. Also, I believe it probable that forms of parasitism other than inquilinism will be discovered. A likely possibility is temporary social parasitism. The peculiar condition of *P. inquilina,* in which a few minor and major workers still persist, could well indicate a recent transition into a state of inquilinism from temporary social parasitism. *P. microgyna,* which has a small body size but is otherwise very little modified anatomically, might be a still active temporary social parasite.

Finally, the generic-level synonymy of the extreme species *Pheidole (= Bruchomyrma) acutidens* and *Pheidole (= Anergatides) neokohli,* which even the conservative systematist W.L. BROWN had resisted, has been proposed for the following reason. It is assumed (on sound anatomical and biogeographic evidence) that all of the nine parasitic species are derivatives of *Pheidole,* independently evolved, and owe their common character states — the "parasitic syndrome" — to parallel evolution. If all three of these inferences are correct, it is difficult to justify the separation of even the most extreme species *(acutidens, kohli,* and *parasitica)* as different genera. The three display a morphocline in the critical characters of mandibular and antennal reduction and postpetiolar widening, while various of the other 6 species possess intermediate states and combinations of states linking the three extreme forms and most free-living *Pheidole.* It would be equally incorrect to combine the extreme species into a single genus, in spite of their superficial similarity, because this entity would then of course be polyphyletic, an arrangement forbidden by modern systematic practice.

If any of the assumptions just noted proves incorrect, the generic synonymy should be reconsidered. In the meantime, the prudent course seems to be to place all of the social parasites of *Pheidole* within the genus *Pheidole,* even if it means joining some forms that are radically different in anatomical characters ordinarily used in generic classification. Such are the unavoidable complications of phylogenetic classification.

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